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Contour feather moult of Ruffs *Philomachus pugnax* during northward migration, with notes on homology of nuptial plumages in scolopacid waders

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Among the sandpiper family Scolopacidae, the Ruff *Philomachus pugnax* combines a large seasonal change in the appearance of the plumage with a very pronounced sexual plumage dimorphism. Studies on the east and south African wintering grounds of Ruffs indicate that before northward migration at least the males moult (part of) their basic (winter) plumage into a kind of alternative plumage. We studied the details of the subsequent moult into a final (supplemental) breeding plumage by quantifying the presence of three feather types – (1) winter (basic), (2) striped (alternate) and (3) breeding (supplemental) – in breast feather samples of 1441 Ruffs captured on staging areas in The Netherlands during northward migration in 1993–97. Ruffs arriving in March show a mix of winter and striped feathers. In April, the ‘breeding feather’ type appears in both male and female Ruffs, and partially takes the place of winter feathers as well as striped feathers in males, and winter feathers only in females. The presence of three plumages in Ruffs is thus confirmed for males, but also occurs in female Ruffs and in Bar-tailed Godwits *Limosa lapponica*. We suggest that striped feathers represent the ‘original’ alternative plumage feather type of the sandpiper family and that the showy feathers of the, in the European literature fortuitously appropriately named, ‘supplementary plumage’ represent an additional feather generation. Such colourful nuptial plumages could thus be derived characters that have evolved independently in several scolopacid genera, presumably under particularly strong sexual selection pressures.

Shorebirds, and especially the sandpiper family Scolopacidae, show fascinating variation between species in the extent of the seasonal change in plumage appearance, and a variety of moult strategies to get from one plumage type into another (Cramp & Simmons 1983, Chu 1994, Higgins & Davies 1996, Piersma *et al.* 1996). However, the available descriptions are incomplete and the terminology is confusing (Higgins & Davies 1996: 16–17). This is an obstacle to the interpretation of the functional significance and evolution of the various moult strategies (Thompson & Leu 1994), an issue that has not been much explored in this group of birds (but see Chu 1994). Although

the naming of moults and plumages often implicates (evolutionary) homologies (Donoghue 1992) in suggestive ways, the terminologies carried by the different handbooks (Glutz von Blotzheim *et al.* 1975, Cramp & Simmons 1983, Higgins & Davies 1996) are conflicting and are never as explicit about their evolutionary connotations as they should be (Humphrey & Parkes 1959, Rohwer *et al.* 1992). We discuss the contour feather moults and plumages of Ruffs *Philomachus pugnax* before and during their migration from the African wintering to the northern breeding grounds. Our observations lead on to suggestions about homologies among successive feather generations carried by adult sandpipers, and thus, about their evolution.

With the exception of the monomorphic snipes (subfamilies Scolopacinae and Gallinagoninae), most

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members of the Scolopacidae show some degree of intra- and interspecific variation in plumages (Piersma *et al.* 1996). We have tried to capture part of this variation in Figure 1, by plotting the extent of species-specific sexual plumage dimorphism against the extent of seasonal change in the plumage of males. Although the majority of species show little sexual plumage dimorphism in the breeding season, there are only few species other than the snipes (not shown in Fig. 1) that are truly monomorphic with respect to the plumage carried during breeding and non-breeding seasons. The Ruff not only demonstrates exceptional interindividual variation in male breeding plumages (van Rhijn 1991), it is also an outlier with respect to both sexual and seasonal dimorphism (Fig. 1). In no other sandpiper is there so much difference between the plumage carried in the non-breeding and breeding seasons, and in which the nuptial plumages of males and females differ so much.

This makes the Ruff an interesting candidate for a detailed examination of moults and plumages, and several authors have seized the opportunity (Kozlova 1957, Stresemann & Stresemann 1966, Drenckhahn 1968, Schmitt & Whitehouse 1976, Pearson 1981, Koopman 1986, OAG Münster 1991). These, and additional museum studies by 'handbook workers', indicate that adult male Ruffs show three contour feather generations per year (summaries in Glutz von Blotzheim *et al.* 1975, Cramp & Simmons 1983, Scheufler & Stiefel 1985,): a non-breeding plumage, a breeding plumage and a supplementary (or display) plumage, respectively (terminology after Cramp & Simmons 1983, Higgins & Davies 1996). According to most authors, females, unlike males, would only show the first two plumages. The timing of the moults is roughly as follows. During southward migration, most Ruffs complete a moult from the supplementary into the non-breeding plumage (OAG Münster 1991). When they arrive on the African wintering areas, some birds still need to complete this moult, especially females (Schmitt & Whitehouse 1976, Pearson 1981). In January–April, the birds moult part of the greyish contour feathers of the non-breeding plumage into the slightly more colourful ones of the breeding plumage (*sensu* Cramp & Simmons 1983), and females do likewise, if somewhat later (Pearson 1981). During northward migration at temperate staging sites, males develop the supplementary plumage, consisting of the long, colourful and variable feathers of ruff and tuft, and of the less acknowledged scapulars and tertials (Drenckhahn 1968, van Rhijn 1991). Some of the females also develop colourful breast feathers and

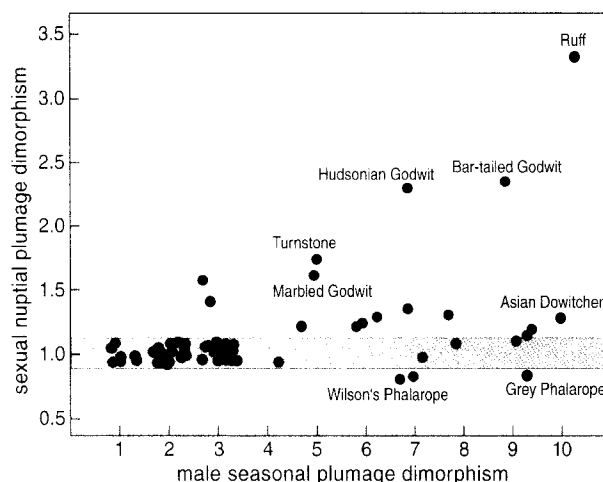


Figure 1. Variation in seasonal (x-axis) and sexual (y-axis) plumage dimorphism in scolopacid waders (family Scolopacidae, except Scolopacinae and Gallinaginae). This graph is based on scores of the variation in plumage in 61 sandpiper species. The scores are subjective assessments of the percentage of plumage that looks substantially different when breeding to how it looks during the non-breeding season. For each of the species, the plates in Hayman *et al.* (1986) and del Hoyo *et al.* (1996) were used to assign scores for the plumages of males and females during the breeding season ranging from 1 (no difference between basic plumage carried in non-breeding season) to 10 (most extreme difference between plumages in breeding and non-breeding season, as in male Ruff and in male Asian Dowitcher *Limnodromus semipalmatus*). The score for males (plotted along x-axis) was then divided by the score for females, and the resulting ratio plotted on the y-axis. Note that plotted points were 'jittered' to avoid overlap; thus, scores for sexual plumage dimorphism of 1 (i.e. no dimorphism) are all included in the shaded range.

scapulars (Cramp & Simmons 1983).

We studied Ruffs at a temperate staging area in The Netherlands, trying to quantify the presence of different feather generations objectively by collecting small samples of breast feathers in captured individuals (cf. Jukema & Piersma 1987, Piersma & Jukema 1993). After describing seasonal changes in the occurrence of different feather types in males and females, a comparison with another migrant scolopacid wader, the Bar-tailed Godwit *Limosa lapponica*, is used as a basis to discuss the homologies among feather generations and plumages in the sandpiper family.

METHODS

In March–May 1993–97, Ruffs were captured on grassland with a traditional netting technique, involving the 3.5 × 25 m and largely wind-powered 'wilsternet' (golden-plover net) and stuffed Golden Plovers

Pluvialis apricaria as decoys to attract Ruffs to the net-area (see Koopman & Hulscher 1979 for a detailed description of the technique). All catches were made in the province of Friesland, The Netherlands, especially in meadows near the towns of Workum and Hindeloopen (52°57'N, 05°25'E). Upon capture, each bird was ringed, weighed to the nearest gram using Pesola spring-balances, and maximum wing-length was measured to the nearest millimetre using a stopped ruler (Jukema *et al.* 1995). Being strongly dimorphic in size, wing-lengths of Ruffs fell into two distinct groups without overlap. Birds with wings shorter than 170 mm were considered females, whereas those with wings longer than 178 mm were considered males (Jukema *et al.* 1995).

A small sample of 10–30 breast feathers (average over 1441 sampled Ruffs: 21.5 feathers/bird) was plucked from each bird and stored in a numbered envelope. As the feathers were pulled out at their base, there will be no collection bias with respect to feather length or feather type. The feather sampling location at the midbreast (see Jukema & Piersma 1987: Fig. 1) was just inside the colourful ruff of males. No individual was sampled more than once. The feathers of each sample were assigned to one of three categories and were counted. We distinguished (Fig. 2): (1) winter feathers (greyish feathers with few marks other than a slightly darker mid-band and light fringes), (2) striped feathers (feathers with a brown-grey base and a series of up to three brown-grey coloured bars, the light-coloured spaces between the bars usually showing increasingly intense buff colours towards the feather edge) and (3) breeding feathers (heavily pigmented, or pure white, feathers showing a variety of colours and patterns, and mainly in males, being of a larger size than either the winter or the striped feathers). Note that in some satellite males (Hogan-Warburg 1966, Lank *et al.* 1995) breast feathers may be white throughout the year (van Rhijn 1991); such white feathers were by necessity assigned to the 'breeding feather' category. Otherwise, as there was hardly any overlap in their characteristics, the three feather types were easy to tell apart.

RESULTS

Half of the feathers of males arriving in The Netherlands in early March consisted of striped feathers, the other half were winter feathers (Fig. 3). The few breeding feathers found were mostly white and probably indicative of satellite males. Until early April, very few of the feathers consisted of the

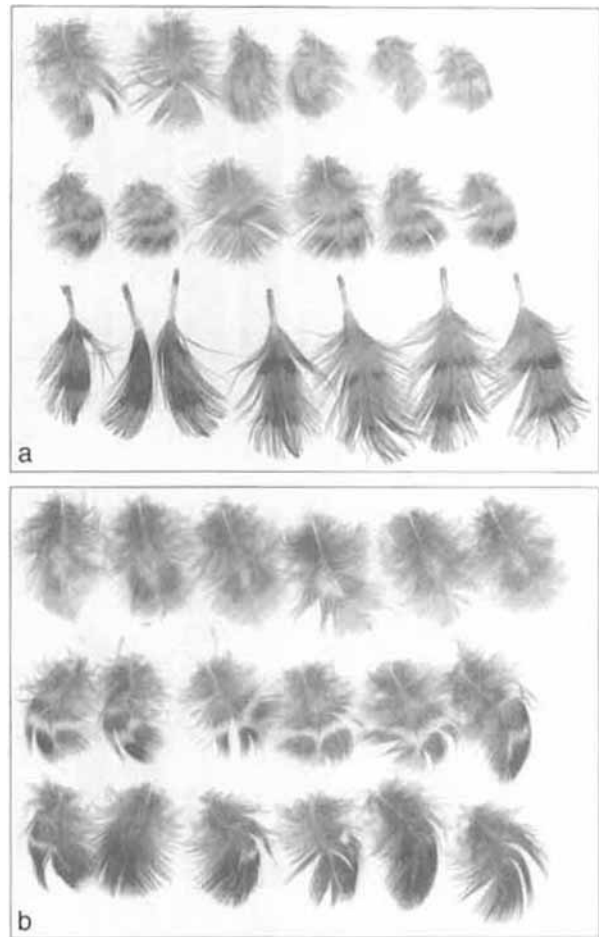


Figure 2. The three contour feather types in male (a) and female (b) Ruffs. In both panels, the top row gives the 'winter feathers', the middle row the 'striped feathers' and the bottom row the 'breeding feathers'. Note that the breeding feathers of the male show waxy sheaths and were still growing when plucked. The feather samples illustrated were collected from a male ringed with Arnhem-ring No. 1.310.623 and a female ringed No. 1.310.621, both on 6 May 1997. Note that the sizes of male and female feathers cannot be directly compared, as the photograph of female feathers has a larger magnification.

breeding type, but from then onwards breeding feathers gradually replaced most of the winter and striped feathers. By early May, 80% of the sampled breast feathers consisted of the breeding type, with winter and striped feathers contributing a mere 10% each.

Females arrived about three weeks after the males on the Frisian staging areas (Jukema *et al.* 1995), but they arrived with similar proportions of winter and striped feathers (50% each, Fig. 4). Breeding feathers were scarce in March and April but, by mid-May, 30% of the breast feathers were of the breeding type (Fig. 4A, 4C). That the proportion of striped feathers increased

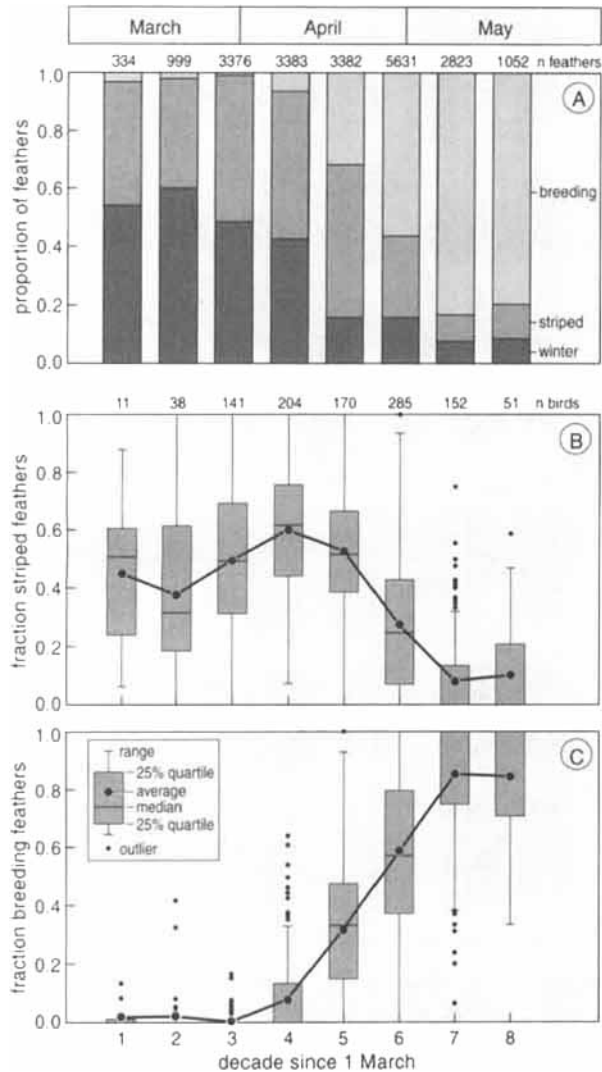


Figure 3. Seasonal changes in the breast feather types of male Ruffs staging in The Netherlands. (A) Overall feather composition. (B, C) Average and distribution of the individual fractions of striped and breeding feathers, respectively. In each panel, the closed dots give the average fraction, and the boxes indicate median, upper and lower quartiles, range and outliers as indicated by the insert. Sample sizes (n) are indicated for feathers (total number examined) in A and individual birds (number of samples taken) in B.

rather than decreased in the course of spring (Fig. 4B), suggests that winter feathers rather than striped feathers were replaced by breeding feathers, but the increasing proportion of striped feathers could also indicate that later arriving females have performed more prealternate moult than birds that leave early. In any case, neither in males nor in females were any winter or striped feathers ever found with waxy sheaths at the feather base (as the breeding feathers in Fig. 2a),

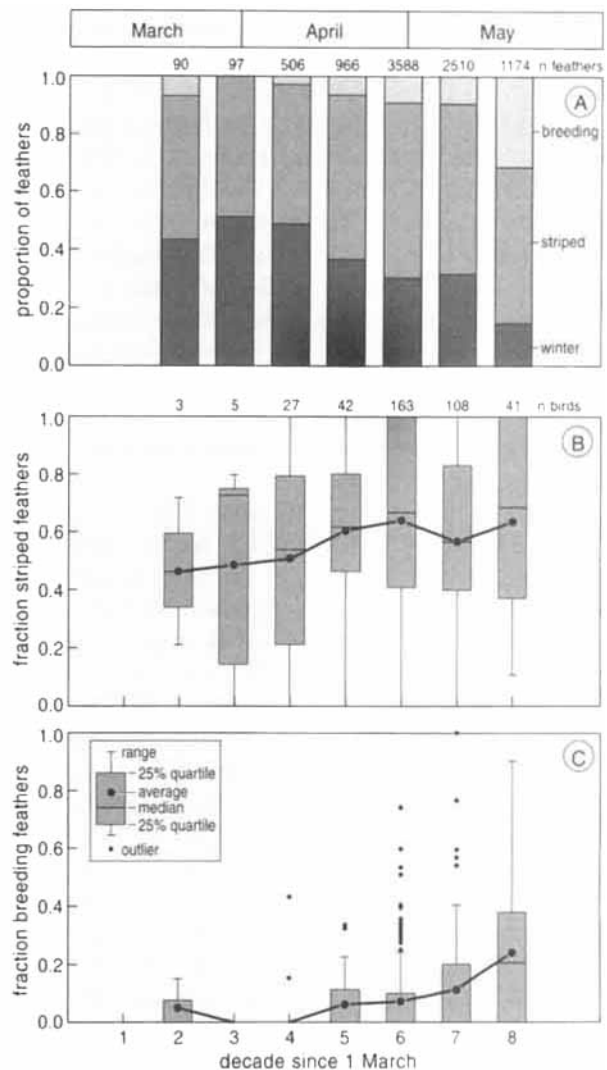


Figure 4. Seasonal changes in the breast feather types of female Ruffs staging in The Netherlands. (A) Overall feather composition, (B) individual fractions of striped feathers and (C) individual fractions of breeding feathers. See caption to Figure 3 for conventions.

indicating that these feather types are never grown during stopover in The Netherlands.

DISCUSSION

We are able to confirm Pearson's (1981) observations that, before northward migration from Africa, male and female Ruffs undergo a partial moult into a 'breeding plumage' (*sensu* Cramp & Simmons 1983), even though Sénégal in West Africa rather than the Rift Valley in East Africa is the source area of the Ruffs migrating through The Netherlands (OAG Münster

1989). We are also able to confirm the suggestion that these temporary 'striped feathers' that replace part of the 'winter feathers' in Africa are themselves replaced during the stopover in The Netherlands before onward migration to North European and West Siberian breeding grounds (van Rhijn 1991).

The extent to which the population changes in feather type composition documented in Figures 3 and 4 reflect similar changes at the individual level is not entirely clear. Although the studies in March–May cover the entire period that Ruffs are common in Friesland, undoubtedly there is turnover in the population (Jukema *et al.* 1995). This would mean that rates of change in the proportions of different feather types would underestimate rates of change in the proportions shown by individuals (see Zwarts *et al.* 1990: Fig. 1). Although based on observations over only three of the 12 months of the year, we were able to confirm that male Ruffs show (at least) three contour feather generations in the course of a year. This may also be true for most females, even though we have not been able to demonstrate unambiguously that striped feathers of females are replaced by breeding ones. Instead, winter feathers may be directly replaced by breeding feathers; such skipping of the striped feather generation has indeed been observed in captive Reeves (D.B. Lank pers. comm.).

Thus, the general scheme is that the non-breeding plumage, indicated by the winter feathers, becomes replaced by a breeding (alternate) plumage indicated by the presence of both winter feathers and striped feathers upon arrival in The Netherlands. During the

stopover, the winter and striped feathers on the breast are (partially) replaced by the breeding feathers of the supplementary (supplemental) plumage. Although since the publication by Stresemann and Stresemann in 1966, everybody has more or less agreed on this moulting scheme (at least for males), the way in which the plumages have been named and interpreted have varied considerably from author to author (Table 1). Whereas Stresemann and Stresemann (1966) and Schmitt and Whitehouse (1976) regarded the plumage represented by striped feathers as a second non-breeding plumage, all other authors assigned it to either a prebreeding or a breeding plumage. Based on the fact that before northward departure from West Africa Ruffs moult some of their breast and belly contour feathers, as well as the feathers of the mantle, scapulars, tertials and some tail feathers, Kozlova (1957) and Cramp and Simmons (1983) considered the striped feathers to represent a 'true' breeding plumage, with the breeding feathers representing a supplementary plumage. We can confirm that Ruffs arrive with fresh feathers in the dorsal feather tracts (pers. obs.), and that in most males and some females some of these feathers (notably the scapulars and tertials) are replaced again during the stopover in The Netherlands.

The interpretation of C.S. Roselaar in Cramp and Simmons (1983), which was followed in Higgins and Davies (1996), would seem to imply that the striped feathers of Ruffs are homologous to the rusty-red feathers of the breeding plumage of Bar-tailed Godwits. Yet, this species arrives from the West

Table 1. Review of the terminology used in the primary and secondary literature to assign the different feather generations carried by adult male Ruffs in the course of the year, together with the suggested terminology based on Humphrey & Parkes' (1959) system on the top line.

| Authority | Basic plumage | Alternate plumage | Supplemental plumage |
|--|---|---|------------------------------------|
| Stresemann & Stresemann (1966) | Erstes Schlichtkleid (‘first cryptic plumage’) | Zweites Schlichtkleid (‘second cryptic plumage’) | Brutkleid (‘breeding plumage’) |
| Glutz von Blotzheim <i>et al.</i> (1975) | Ruhekleid (‘resting plumage’) | Pränpupialkleid (‘prenuptial plumage’) | Prachtkleid (‘display plumage’) |
| Schmitt & Whitehouse (1976) | First non-breeding plumage | Second non-breeding plumage | (Breeding plumage) |
| Pearson (1981) | Winter plumage | First summer plumage | Second summer plumage |
| Cramp & Simmons (1983) | Non-breeding plumage | Breeding plumage | Supplementary plumage |
| Scheufli & Stiefel (1985) | Ruhekleid (‘resting plumage’) | Pränpupialkleid (‘prenuptial plumage’) | Brutkleid (‘breeding plumage’) |
| van Rhijn (1991) | Non-breeding plumage | Breeding or prenuptial plumage | Nuptial plumage |

African wintering grounds with a colourful plumage that partially consists of striped feathers too, and the striped feathers of godwits are very similar in appearance to those of Ruffs (see Piersma & Jukema 1993: Fig. 1). The striped feathers presented an enigma to Piersma and Jukema (1993). However, noting that the feathers that comprise the breast and belly parts of the breeding plumages of scolopacids with more cryptic nuptial plumages, such as many shanks and curlews (Tringinae; e.g. Paulson 1993), are actually quite similar to the striped feathers of Ruffs and Bar-tailed Godwits, we suggest that striped feathers indeed represent the 'original' breeding plumage feather type of the sandpiper family. The showy feathers of the supplementary plumage thus represent an additional feather generation. The existence of 'three different types of summer-plumage feathers' was also noted in several populations of Black-tailed Godwits *Limosa limosa* by Roselaar and Gerritsen (1991). Note that the 'striped feathers' of Golden Plovers described by Jukema and Piersma (1987) must be different, as they emerge in the course of the breeding season, partially replacing the highly pigmented 'breeding feathers' that in turn replaced cryptic 'winter feathers'.

If the hypothesis about striped feathers representing the original breeding plumage of Scolopacidae is upheld, it is easy to see how the terminology of Humphrey and Parkes (1959) should be applied in the case of Ruffs, so that the terminological confusion emanating from Table 1 can be dispelled. The winter feathers form the *basic* plumage, the striped feathers mark the existence of the *alternate* plumage and the breeding feathers represent a *supplemental* plumage. In Bar-tailed Godwits the alternate plumage was hitherto unrecognized, and what we now consider to be the supplemental plumage was regarded as such (Cramp & Simmons 1983, Higgins & Davies 1996). On this basis one could predict that the same sequence of moults and plumages may also occur in several other scolopacids with particularly colourful nuptial plumages (apart from Black-tailed Godwits mentioned earlier, Fig. 1 suggests Hudsonian Godwits *Limosa haemastica*, Asian Dowitchers *Limnodromus semipalmatus* and Grey Phalaropes *Phalaropus lobatus* as candidates). Comparative documentation of different feather generations would help a great deal in bringing the evolutionary history of nuptial plumages of scolopacid waders in perspective.

According to Chu (1994), seasonal plumage change is a derived character within the Charadriiformes, and it may be an evolutionary novel trait which may or may not have been shown by the ancestor of the

Scolopacidae. Although the monomorphic snipes could represent the ancestral pattern within the Charadriiformes (Chu 1994) (Fig. 4A), their plumage monomorphy may also be a derived character (Chu 1994) (Fig. 4B). It is possible that seasonal plumage variation reflects the outcome of the tension between 'natural selection' for crypsis winning in the non-breeding season, and 'sexual selection' for advertisement winning in the breeding season (see Butcher & Rohwer 1989). But if crypsis is important in all seasons, it is also possible that the changing plumages track concurrent changes in the 'crypsis' of the ambient environments (cf. Jukema & Piersma 1987). The latter possibility is perhaps not very likely for the showy male Ruffs. Ruffs, and also Bar-tailed Godwits, may have been under such intense sexual selection pressure that a feather type evolved that is even less cryptic than the striped feather of the usual alternate plumage, i.e. the colourful feathers of the supplemental plumage. Note that this view was independently formulated in 1957 by E.V. Kozlova but was published in Russian and not known by western ornithologists. Sexual selection pressures leading to the evolution of a supplemental plumage may be linked to performance-aspects of long-distance migration (Piersma & Jukema 1993, Fitzpatrick 1994).

If the genetic control of such moulting strategies is not completely sex-linked, it is less surprising that the more cryptic female Ruffs (the Reeves, that do all the choosing of mates; van Rhijn 1991) should also show partial moult into a supplemental plumage. In this context it is interesting that testosterone implants in non-breeding females lead them to develop supplemental plumage, including large colourful ruff-feathers (D.B. Lank pers. comm.). Castrated male Ruffs fail to develop the showy supplemental plumage, but they do grow a plumage 'characteristic of females in spring' (van Oordt & Junge 1936). The skins of these experimental male Ruffs, kept at the Zoological Museum in Amsterdam, show that the latter plumage consists of striped feathers (C.S. Roselaar pers. comm.). If the finding that the prealternate moult needs no hormonal triggering indicates that this moult is very 'hard-wired', the absence of strong negative selection pressures may have prevented the alternate plumages from disappearing, even if they are no longer functionally important. An alternative argument would be that, by definition, alternate plumages are under direct sex-hormonal control (D.P. Whitfield pers. comm.). In this case, the striped feather generation would represent a supplement to the basic plumage, and Stresemann and Stresemann's (1966) position would be vindicated.

Equally, the line of argument followed so far would collapse. Experimental studies on body moult across a variety of shorebird species using hormone implants are probably required to evaluate these alternatives.

In the words of Thompson and Leu (1994), 'insights into the evolution of molts and plumage patterns can only be gained by identifying homologous molts and plumages among related taxa'. By pointing out that, on the wintering areas, winter feathers are partly replaced by striped feathers in both Ruffs and Bar-tailed Godwits (distinct lineages within the Scolopacidae; Strauch 1978) and that such feathers may represent the original alternate plumage of the sandpiper family, we hope to have made a start in clarifying the terminological confusion that hinders progress in reconstructing the evolutionary processes that shape the life-histories of this fascinating group of birds.

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